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Connectivity and vagility determine spatial richness gradients and diversification of freshwater fish in North America and Europe

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The latitudinal species richness gradient (LRG) has been the subject of intense interest and many hypotheses but much less consideration has been given to longitudinal richness differences. The effect of postglacial dispersal, determined by connectivity and vagility, on richness was evaluated for the species-poor European and North American Pacific and species-rich Atlantic regional freshwater fish faunas. The numbers of species, by habitat, migration and distributional range categories, were determined from regional species lists for these three realms. The current orientation and past connections of drainage channels indicate that connectivity is greatest in the Atlantic and least in the Pacific. With increasing connectivity across realms, endemism decreased and postglacial recolonization increased, as did the LRG slope, with the greatest richness difference occurring between southern Atlantic and Pacific regions. Recolonizing species tended to be migratory, habitat generalists and from families of marine origin. Diversification, as indicated by species/genus ratios, probability of diversification, taxonomic distinctness and endemicity, declined with increasing latitude in all realms and was least in Europe. Richness patterns are consistent with an LRG driven by the time available for postglacial recolonization and by differences in dispersal ability, with richness differences across realms reflecting differences in dispersal and diversification. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2015, **116**, 773–786.

ADDITIONAL KEYWORDS: dispersal limitation – extinction – history – latitudinal richness gradient – postglacial recolonization – speciation.

INTRODUCTION

Ecological, biogeographic and evolutionary mechanisms have been proposed to account for the latitudinal richness gradient (LRG). Species richness and LRG slopes also differ across continental and other geographic units (Hillebrand, 2004) but much less attention has been paid to these differences. Geographic unit slope differences might arise because latitudinal climate gradients differ geographically, the responses of faunas to a given gradient differ (Gouveia *et al.*, 2012) and/or barriers to dispersal might prevent species reaching equilibrium with climatic conditions (dispersal limitation).

Long-term spatial variation in richness is determined by speciation, extinction and dispersal (Mittelbach *et al.*, 2007), but few people have addressed the role of all three processes (Wiens *et al.*, 2009). The time-for-speciation hypothesis (Stephens & Wiens, 2003) invokes the greater duration of habitable (tropical) environments to account for the LRG while niche conservatism, the tendency to retain ancestral niche characteristics, limits range expansion of, usually tropical, taxa. Diversification (speciation – extinction) rate differences can also generate spatial variation in richness. Source-sink (latitudinal gradients in speciation and dispersal rates), out-of-the-tropics (gradients in speciation, extinction and dispersal), and Wallace (gradients in extinction and possibly dispersal) models have been proposed (Roy & Goldberg, 2007). Out-of-the-tropics, time-for-speciation and niche conservatism hypotheses have found support in a variety of studies of marine and terrestrial taxa (Mittelbach *et al.*, 2007; Wiens *et al.*, 2010; Jansson, Rodríguez-Castañeda & Harding, 2013) but there have been no studies of freshwater fish. These models do not consider differences between species in vagility, the propensity to cross barriers,

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but dispersal limitation can also generate an LRG over geologically short, for example postglacial, time periods. While this factor cannot be a global explanation for the LRG, dispersal limitation is a potentially important factor for some taxa, such as freshwater fish in recently glaciated areas (Leprieur *et al.*, 2009; Schleuter *et al.*, 2012; Padial *et al.*, 2014). Dynesius & Jansson (2000), and subsequently Jocque *et al.* (2010), argued that greater climatic variability at high latitudes favours generalism, vagility and large range sizes, traits which reduce extinction risk and, by increasing gene flow, speciation rates. They suggested that these factors generate the LRG and presented evidence in support of this climate variability, dispersal, generalism (CDG) framework, garnered from a wide range of taxa, but not from within a single taxon.

Isolation, by reducing gene flow, increases the chances of speciation (Coyne & Orr, 2004) and, consequently, should increase endemic species richness. Furthermore, extinctions are more likely in isolated populations subject to environmental disturbances such as glaciations because of reduced immigration from, and migration to, more favourable areas (Brown & Kodric-Brown, 1977; Leibold *et al.*, 2004). For fish in freshwater networks, isolation is determined by channel connectivity, that is possible dispersal pathways, and by vagility. Connectivity usually changes on relatively long time scales, for example by river capture, flow reversal, marine incursion, climatic change. Isolation can be absolute, for example impassable waterfalls within drainages, but is usually species-dependent, for example limited by marine barriers between drainages or by a sluggish, turbid, lowland river separating clear, fast flowing, upland, tributaries. Vagility varies with migratory capacity, tolerance of saline conditions and habitat preference in freshwater fish (Griffiths, 2010; Tedesco *et al.*, 2012). Across-catchment dispersal in primary, saltwater-intolerant, freshwater species can occur following connectivity changes from, for example, sea level falls during glaciations or river capture while, within catchments, spatial variation in habitat is more likely to limit habitat specialist species than generalists.

Here, I examine the contributions of connectivity, dispersal and diversification to realm differences and latitudinal trends in the richness of native freshwater fish species in Atlantic and Pacific realms of North America (to the east and west of the Continental Divide respectively) and Europe: previous investigations have examined intracontinental patterns (e.g. Hocutt & Wiley, 1986; Griffiths, 2006, 2010). North America and Europe differ in shape (longitudinal range is greatest in arctic North America but least in arctic Europe), connectivity (Atlantic > Europe > Pacific, see Methods) and climate, all of which are likely to affect species richness patterns. The LRG is usually correlated with current and/or past climatic gradients (e.g. Oberdorff *et al.*, 2011). There have been few inter-continental (as opposed to global) comparisons, but these offer the possibility of better resolution of the roles of historical (connectivity, glaciation) and evolutionary (speciation, extinction) factors on species richness and composition by reducing nonstationary effects (Gouveia *et al.*, 2012) from, for example, realm differences in climatic relationships (Griffiths, McGonigle & Quinn, 2014).

Freshwater fish richness is greater in the Atlantic than in Pacific and European realms (Smith, 1981; Mahon, 1984; Moyle & Herbold, 1987). Oberdorff, Hugueny & Guégan (1997) showed that much of the variation in richness was correlated with climatic factors but they also found a continental effect which they considered reflected the role of historical events. Subsequent analyses found that climatic and historical factors were important richness predictors globally, and for North America and Europe (Knouft & Page, 2011; Oberdorff *et al.*, 2011; Griffiths *et al.*, 2014). Globally, Dias *et al.* (2014) showed that, after controlling for climatic effects, historically connected river basins had greater fish species richness but lower endemism and beta diversity than isolated catchments. However, most studies of connectivity have focussed on single species and/or small areas (e.g. Sullivan & Watzin, 2009; Carrea *et al.*, 2014) and I am unaware of any examining connectivity effects at the realm scale.

Long-term disturbances have occurred from, for example, tectonic events changing hydrography, particularly in the Pacific realm and, across all realms, from climatic events such as glaciations in northern regions and increased aridity since the last glaciation in southern regions (Minckley, Hendrickson & Bond, 1986; Smith & Miller, 1986; Roberts, 1998). In addition to causing regional extinctions, glaciation affects landscape topography and surface deposits, with effects on fish faunas at taxonomic and functional levels (Jacquemin & Pyron, 2011). Aridity has resulted in extinctions in some areas (particularly the Pacific) but, by subdividing catchments, also favours speciation (Smith, 1981; Hocutt & Wiley, 1986; Oberdorff, Lek & Guégan, 1999). Isolation should decrease with increasing latitude because of: (1) increasing connectivity (increasing aridity in southern regions has fragmented catchments while extensive proglacial lakes permitted crosscatchment movements in the north); and (2) increasing vagility (Griffiths, 2010), suggesting that disturbance effects will be greater in southern areas.

Previous work on fish found in freshwaters in North America and western Europe (Griffiths, 2006,

2010; Griffiths *et al.*, 2014) has shown latitudinal changes in climatic variability, in the proportions of generalists and migrants and in range size (Rapoport's rule), and that generalists are more likely to be migrants, consistent with the CDG framework. Here I test the effects of within and, for the first time, across-realm connectivity on fish species richness and composition, and whether speciation and extinction contribute to latitudinal trends. Specifically,

1 With increasing connectivity across realms, the percentage of recolonizers (species occurring in both unglaciated and glaciated areas) should increase and endemism decrease. If current connectivity plays the dominant role in determining distribution then species composition should change less rapidly with spatial separation, and similarity be greater, within than across drainage basins (Nekola & White, 1999). If vagility plays a significant role in determining distribution then compositional differences within a catchment for resident (non-migratory) species should be greater, and mean range sizes smaller, than for migrants.
2 If dispersal limitation is important LRG slopes should differ between species with different migratory capacities. Postglacial recolonization ability should vary with migratory capacity, tolerance of saline conditions and habitat preference.
3 Species/genus ratios should be greater and taxonomic distinctness, a measure of the relatedness of species assemblages (Clarke & Warwick, 1998), lower in southern areas if diversification is more likely to occur there. If the LRG is affected by extinctions in, or limited recolonization from, the south, the richness slope should decline with decreasing realm connectivity. If the LRG is driven by speciation in, and dispersal from, the tropics (the out-of-the-tropics model) then tropical/subtropical taxa should extend through North America, particularly in the Atlantic realm.

The focus is on late Quaternary events: by the start of this period the present-day freshwater fish families were established in North America and Europe (Banarescu, 1989; Ross, 2013).

METHODS

Data

Species presence/absence lists were compiled for regions of North American from the Isthmus of Tehuantepec northwards from published information (Hocutt & Wiley, 1986; Page & Burr, 1991; Miller, Minckley & Norris, 2005), and revised since Griffiths (2010), and for Europe west of the Urals and north of Turkey (Fig. 1). In many instances these regions are based on drainage basins but the Mississippi and Danube basins are subdivided, while some regions contain several basins. Some comparisons were made at the continental scale. However, since there are large-scale differences within North America I use the term realm for those areas east and west of the Continental Divide in North America (Atlantic, Pacific) and for Europe. Diversification analyses were conducted at this scale but, when analysing connectivity, the Atlantic realm is subdivided into Mississippi and extra-Mississippi Basin sub-realms to reflect present-day connectivity differences.

Physical barriers are assumed, in general, to pose less of an obstacle to distribution within than across catchments. Accordingly, the Mississippi Basin is the most connected area of the Atlantic realm, but has exchanged species with northern catchments and southern faunal refuges of the extra-Mississippi Atlantic regions during glacial periods (Hocutt & Wiley, 1986). I assume extra-Mississippi regions to be more connected than European regions. Extensive proglacial lakes permitted cross-catchment recolonization as the ice retreated in both realms but Mediterranean Europe is separated from the rest of the realm by mountain barriers while many regions are at least partially isolated by marine barriers. Oberdorff *et al.* (1997) suggested that postglacial recolonization was more likely in the north-south trending rivers of eastern North America compared to a mainly east-west orientation of European (and Pacific) rivers. Consequently, the current orientation and past connections of drainage channels indicate that connectivity decreases in the sequence Mississippi Atlantic > extra-Mississippi Atlantic > Europe > Pacific. Others (Mahon, 1984; Hocutt & Wiley, 1986; Moyle & Herbold, 1987; Oberdorff *et al.*, 1997; fig. 5 in Smith *et al.*, 2010) have also noted similar, across-realm rankings in connectivity for freshwater fish.

Taxonomic definition and resolution will affect estimates of the number of species. Recent estimates have been relatively stable in North America (from about 950 species (Hocutt & Wiley, 1986) to 1061 (Ross & Matthews, 2014). However, in Europe Kottelat (1998) recognised 358 native species while Kottelat & Freyhof (2007) noted 525 species, much of the 47% increase resulting from changes in taxonomy rather than new discoveries. In the most extreme case, Kottelat & Freyhof split the 15 salmonids listed by Maitland (2000) into 112 species, most of which were restricted to single lakes. In the present analysis I have followed the Maitland classification for salmonids (see Etheridge *et al.*, 2012 for a test which rejects the Kottelat & Freyhof classification of British *Coregonus*) but mainly adopted the Kottelat

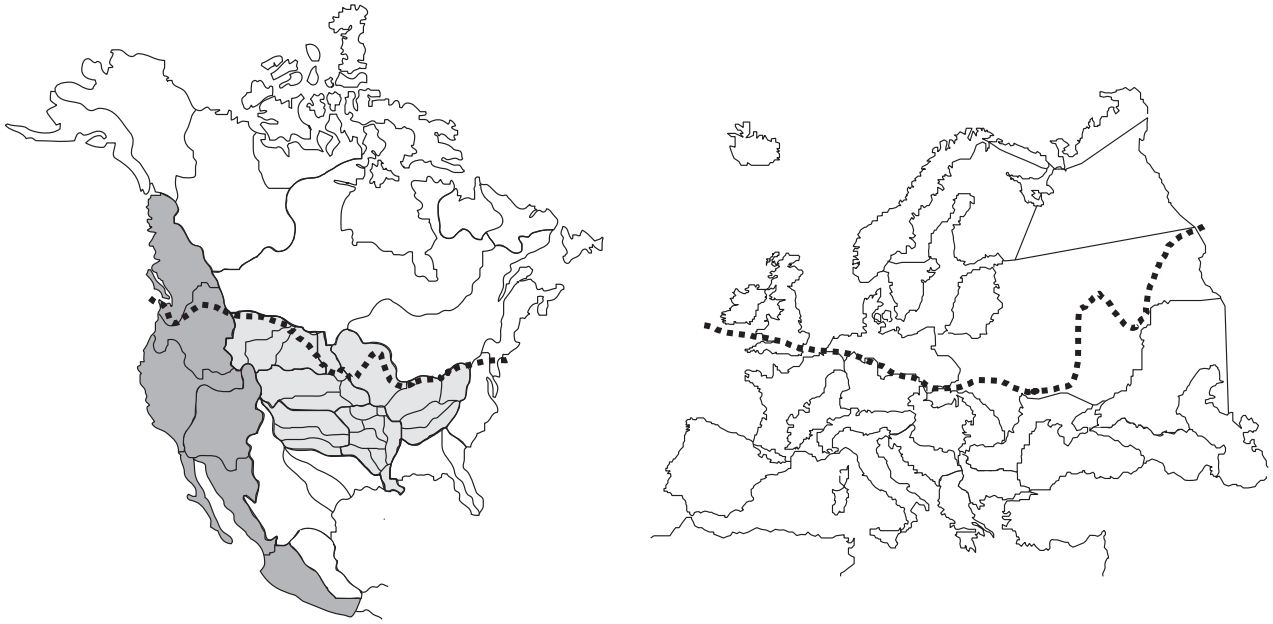

Figure 1. Regions in the Pacific (dark shading) and Atlantic (left) and European (right) realms (not drawn to the same scale). The light shaded area in the Atlantic realm denotes the regions comprising the Mississippi Basin. The regions are named in Griffiths (2006, 2010). The dotted lines indicate the approximate southern limit of ice at the last glacial maximum.

& Freyhof listing, although omitting species restricted to single, small, water bodies such as *Clupeonella abrau* (Maljatskij, 1928), *Pelasgus epiroticus* (Steindachner, 1896). This generated a total of 351 species in Europe, the increase from the 272 in Griffiths (2006) resulting mainly from southern region endemics. The conclusions based on this increased species list do not differ in any substantive way from those generated using the earlier more conservative list.

Procedures and categories generally follow those used in Griffiths (2006, 2010). Regions are identified as: (1) glaciated or unglaciated, depending on whether or not they were largely covered by ice at the last glacial maximum; and (2) coastal or inland, rivers in the latter draining to other regions. Using published sources (Hocutt & Wiley, 1986; McDowall, 1988; Page & Burr, 1991; Smith, 1991; Northcote, 1997; Maitland, 2000; Lucas & Baras, 2001; Miller *et al.*, 2005; Kottelat & Freyhof, 2007; Chapman *et al.*, 2012), FishBase (www.fishbase.org) and FishTraits (http://www.fishtraits.info), regional species lists were compiled and species categorised by: (1) habitat preference, as riverine (found only in rivers), lacustrine (found only in lakes), or generalist (occurring in both habitats); (2) migration type, as migratory (migrating between sea and freshwater, along river channels or between rivers and lakes during their life cycle) or resident (non-migratory species); and (3) distributional range, as endemic (found in only one region of a continent) or non-endemic. As spring-dwellers are usually associated with flowing water I classified them as riverine. Recolonization across catchments is more likely in species that can tolerate saltwater: the proportion of species from families of marine ancestry was used as a crude measure of the likelihood of tolerance of saline conditions.

Analyses

The Cochran–Armitage test (Fleiss, 1973) was used to test for trends in species proportions across realms ordered by decreasing connectivity i.e. Mississippi Atlantic > extra-Mississippi Atlantic > Europe > Pacific.

To test if latitudinal richness gradients varied with connectivity, slopes were ranked across realms for each richness grouping (rank 1 = smallest slope) and realm differences tested by analysis of variance (ANOVA): ranks were used because slopes differed across richness groups.

To examine the out-of-the-tropics model, species, in catchments listed in Hocutt & Wiley (1986) with latitudes below 37°N on the Pacific coast and southwest of the Mississippi on the Atlantic coast, were classified by whether the fish belonged to families with North or South American origins. The percentage of species from families with South American

origins was plotted against the latitude of the river mouths to determine how far these species had penetrated into North America. Endorheic basins and marine-origin families were excluded, as were goodeids which, while freshwater, are largely restricted to central Mexico.

Diversification (speciation – extinction) rates might differ between realms and with latitude (Smith *et al.*, 2010). Four indicators of regional diversification were used. Firstly, species/genus (S/G) ratios can increase by diversification (Krug, Jablonski & Valentine, 2008): S/G ratios were calculated from regional numbers of species and genera.

Secondly, in the absence of adequate phylogenetic and fossil data, regional probability of diversification was estimated as the number of genera with two or more endemic species, divided by the number of endemic genera (Kisel & Barraclough, 2010): note that these estimates apply only to unglaciated areas as no endemics occur in glaciated areas (Supporting Information, Table S1). Realm and latitude effects on diversification probability were tested using general linear models with binomial errors (R Development Core Team, 2013).

Thirdly, the taxonomic distinctness of an assemblage, which in well-resolved taxonomies can estimate phylogenetic diversity, is the distance between species in a classification tree (taxonomic levels; species, genus, family, order, class). Taxonomic distinctness and species richness are potentially related over evolutionary time: for example, a decrease in average taxonomic distinctness (avTD) with increasing regional species richness indicates increasing numbers of congeners in species-rich regions, consistent with greater diversification there. Primer 6 software (Clarke & Gorley, 2006) was used to calculate avTD from regional species lists: 95% confidence funnels for taxonomic distinctness were generated by randomising species lists for Atlantic, Pacific and European realms. The strength of the effect was assessed as the observed deviation from random expectation divided by the null model standard deviation.

Finally, endemicity, a measure of endemism corrected for faunal richness, was calculated as the sum of species present in a region, weighted by the inverse of the number of regions where the species occurs, and divided by total regional richness (Crisp *et al.*, 2001; Tisseuil *et al.*, 2013). The AICc model selection procedure (Burnham & Anderson, 1998) was used to decide whether linear or piecewise models better described endemicity–latitude relations: ΔAICc values > 10 indicate essentially no support for the weaker model.

To test if late Cenozoic extinctions varied spatially, I compared the proportion of extinctions (from data in Smith, 1981 and Smith *et al.*, 2002) in taxa characteristic of northern (Salmonidae, Osmeridae, Cottidae) and southern (Cyprinidae, Catostomidae, Ictaluridae, Cyprinodontidae, Centrarchidae) environments.

Most analyses were conducted using Systat 13 Software. Species richness and area were normalised/linearised by logarithmic transformations to the base 10, all percentages were arcsine square-root transformed, and all interval estimates are standard errors. The compositional similarity of fish faunas (from presence/absence data) was measured as Jaccard distances which were then clustered by the flexible β (−0.25) method (McCune & Mefford, 2006). Correlation was assessed by Pearson (r) or, with non-normal data, by Spearman (r_s) correlation coefficients.

RESULTS

Realm differences

Total richness is much greater in Atlantic than in Pacific and European realms (743, 276 and 351 species respectively). Only 11 species are found in both Europe and North America, all with northern distributions. The Atlantic and Pacific realms have 58 species in common: these shared species form an increasing percentage of total richness with latitude (nine 5° latitude bands; $r_s = 0.75$, $P < 0.05$). Species richness did not differ between realms in glaciated regions but was 82% greater in the unglaciated Atlantic than in the Pacific (latitude and area as covariates; glaciated $F_{2,20} = 2.51$, $P > 0.1$, unglaciated $F_{2,42} = 3.45$, $P < 0.05$).

There were significant latitudinal richness trends: richness declined linearly for most categories (Fig. 2A, B; 23/31 declines, 2/31 increases over four realm by eight richness category comparisons, no lacustrine species in the Mississippi Basin) but potamodromous species showed quadratic trends (Fig. 2C; 3/4 realms).

The LRG slope declined with decreasing connectivity (mean ranks across each species category; Mississippi 3.50 ± 0.33, extra-Mississippi 2.57 ± 0.29, Europe 2.33 ± 0.33, Pacific 1.44 ± 0.29; test for linear trend with connectivity $F_{1,31} = 20.39$, $P < 0.001$). Pacific–Atlantic richnesses converged with increasing latitude (mean difference across species groupings in latitudinal slopes, Pacific – Mississippi −0.027 ± 0.008, Pacific – extra-Mississippi −0.021 ± 0.007), so the biggest difference in richness across realms was found at low latitudes.

As expected, the percentage of recolonizing species (species occurring in both unglaciated and glaciated areas) in all species categories increased with increasing realm connectivity (Table 1) and latitude (Fig. 3):

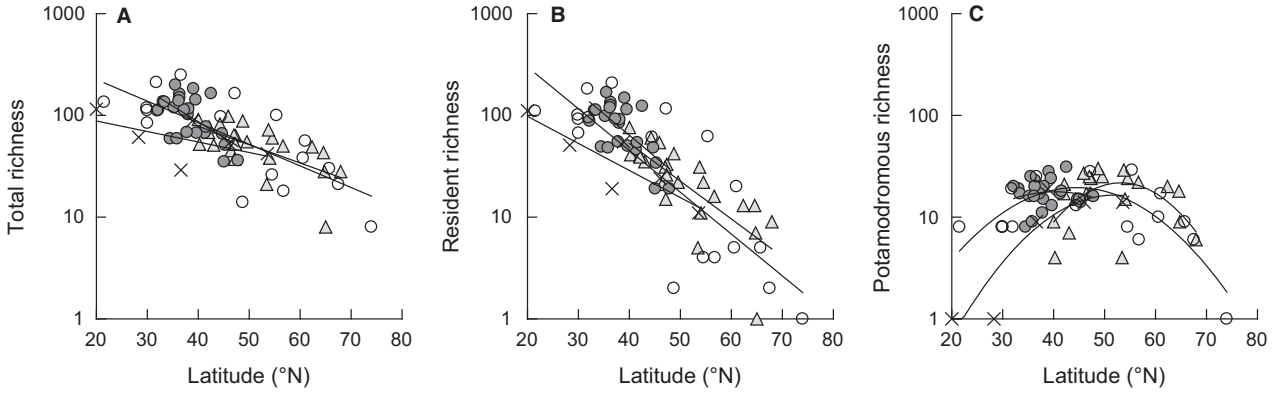

Figure 2. (A) Total, (B) resident and (C) potamodromous regional species richness as a function of latitude for Atlantic (Mississippi regions filled circles, extra-Mississippi regions open circles), Pacific (crosses) and European (triangles) realms.

Table 1 . Summary of differences in area, taxon richness, habitat preference, migration category and endemism across realms, ordered by degree of connectivity

		Atlantic Mississippi	Atlantic extra-Mississippi	Europe	Pacific	*P*-value
Area ($\times 10^6$ km^2)		3.07	14.94	8.75	3.34	
Area unglaciated ($\times 10^6$ km^2)		2.26	4.31	5.61	2.74	
Number of species		339	648	351	276	
Species per 10^6 km^2		110	43	40	83	
	% Unglaciated	45.4	61.1	62.1	84.1	***
	% Recolonizers	54.3	36.6	31.9	15.6	***
Number of genera		82	157	91	98	
Number of families		28	48	21	32	
% riverine		61.5	62.3	52.1	59.3	ns
% riverine	Unglaciated	68.3	81.1	73.2	92.6	***
% riverine	Recolonizers	31.7	18.2	19.1	7.4	***
% generalist		38.5	34.3	41.0	27.6	ns
% generalist	Unglaciated	8.5	24.3	45.8	59.2	***
% generalist	Recolonizers	90.8	73.0	50.7	39.5	***
% lacustrine		0.0	3.3	6.8	13.1	***
% resident		85.8	83.5	78.9	80.4	*
% resident	Unglaciated	52.2	69.7	75.1	94.1	***
% resident	Recolonizers	47.8	28.5	19.5	5.4	***
% migratory		14.2	16.5	21.1	19.6	*
% migratory	Unglaciated	4.2	17.8	13.5	42.6	***
% migratory	Recolonizers	93.8	77.6	78.4	57.4	***
% endemic		19.1	41.2	50.1	66.7	***

P is the significance level from the Cochran–Armitage test for ordered proportions. Unglaciated species are restricted to unglaciated areas, recolonizers are found in unglaciated and glaciated areas. % values for the few species restricted to glaciated areas are not shown. The number of species in each category is shown in Supporting Information (Table S1). *$P < 0.05$, ***$P < 0.001$, ns $P > 0.05$.

within Europe, the percent of recolonizing species increased from the isolated Mediterranean regions to other unglaciated and glaciated regions (38%, 75%, 100% respectively, $F_{2,21} = 181.05$, $P < 0.001$). Across realms the percentage of recolonizers varied with the percentages of species from families of marine origin,

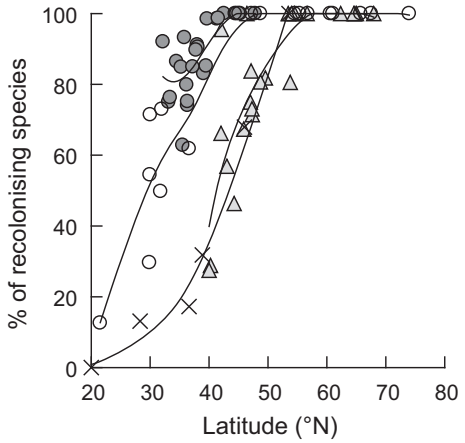

Figure 3. The percentages of species that have recolonized glaciated regions (Mississippi (filled circles), extra-Mississippi (open circles), Pacific (crosses) and European (triangles) realms). Species restricted to glaciated areas were excluded from the calculation.

Table 2 . The percentage of recolonizing species per region varies with the percentages of habitat generalist, migratory species and species from families of marine origin. The least square adjusted means are the arcsine square-root transformed values

Variable	d.f.	MS	*F*-value	*P*-value
Realm	3	844.11	10.40	***
% generalist	1	1784.51	21.99	***
% migratory	1	1741.97	21.47	***
% marine	1	315.56	3.89	*
Error	65	81.13		
R^2		0.84		

Least squares adjusted means

Realm	Means ± SE	*N*
Atlantic Mississippi	79.94 ± 2.36	24
Atlantic extra-Mississippi	67.35 ± 2.57[a]	18
Europe	61.36 ± 2.08[a]	24
Pacific	60.20 ± 4.69[a]	6

[a]Realms with the same letter are not significantly different (Tukey honestly significant difference (HSD)test).
*$P < 0.05$, ***$P < 0.001$. d.f., degrees of freedom; MS, mean squares; SE, standard error.

of generalist and of migratory species (Table 2). Richness slopes were significantly steeper for resident than for migratory and for freshwater than for marine-origin species ($b = -0.036 \pm 0.003$ vs. 0.003 ± 0.002, -0.030 ± 0.003 vs. -0.006 ± 0.002 respectively), consistent with dispersal limitation.

No species from South American families occur north of 34 °N (Supporting Information, Fig. S1) but there is still a strong LRG north of that (Fig. 2A): hence the out-of-the-tropics hypothesis is insufficient to account for the observed LRG gradient. Pairwise Jaccard distances did not change more slowly with spatial separation when both regions were within the Mississippi Basin than when one region was inside and one outside the Basin ($F_{1,704} = 1.48$, $P > 0.2$), suggesting that current connectivity does not determine species distributions. While Jaccard distances are, on average, significantly smaller within Basin than across Basins ($F_{1,705} = 68.62$, $P < 0.001$), many within-Basin comparisons showed greater dissimilarity (Supporting Information, Fig. S2). Within the Mississippi Basin, Jaccard distances for resident species were significantly greater than for migrants (mean pairwise difference 0.133 ± 0.007, $P < 0.001$) and (log) mean range sizes significantly smaller ($F_{1,337} = 48.02$, $P < 0.001$; residents 5.979 ± 0.042, $N = 291$, migrants 6.758 ± 0.104, $N = 48$).

Diversification

The Atlantic has more species and species/genus than the other realms (Table 1), indicating greater diversification there. However, regional S/G ratios did not differ between Pacific and Atlantic realms but were greater in North America than Europe and declined with increasing latitude (continents $F_{1,69} = 10.97$, $P < 0.01$, latitude $F_{1,69} = 24.14$, $P < 0.001$; least squares means North America 1.954 ± 0.058, Europe 1.601 ± 0.085). Similarly, the probability of diversification differed across continents and declined more steeply with latitude in Europe than North America (Supporting Information, Table S3).

Taxonomic distinctness declined steeply with increasing species richness (Supporting Information, Table S2, Fig. 4A, B: slopes Atlantic -8.76 ± 1.25, Pacific -6.39 ± 1.16, Europe -16.27 ± 2.44). Glaciated Atlantic and European regions had greater than expected avTD while it was less in unglaciated regions (Fig. 4C); that is species-rich and unglaciated regions had more congeners than expected.

Endemicity was greatest in less connected and unglaciated regions (Table 3) and increased with declining realm connectivity ($F_{1,65} = 20.02$, $P < 0.001$). It declined rapidly with latitude in unglaciated areas before levelling off in the Atlantic and European realms whereas it declined linearly in the Pacific (Fig. 5; piecewise – linear regressions ΔAICc = −42.88, −21.48, 30.00 respectively). Endemicity was greater in the isolated Mediterranean than in other European regions (0.541 ± 0.046, $N = 4$; 0.164 ± 0.020, $N = 20$ respectively, $F_{1,22} = 56.20$, $P < 0.001$).

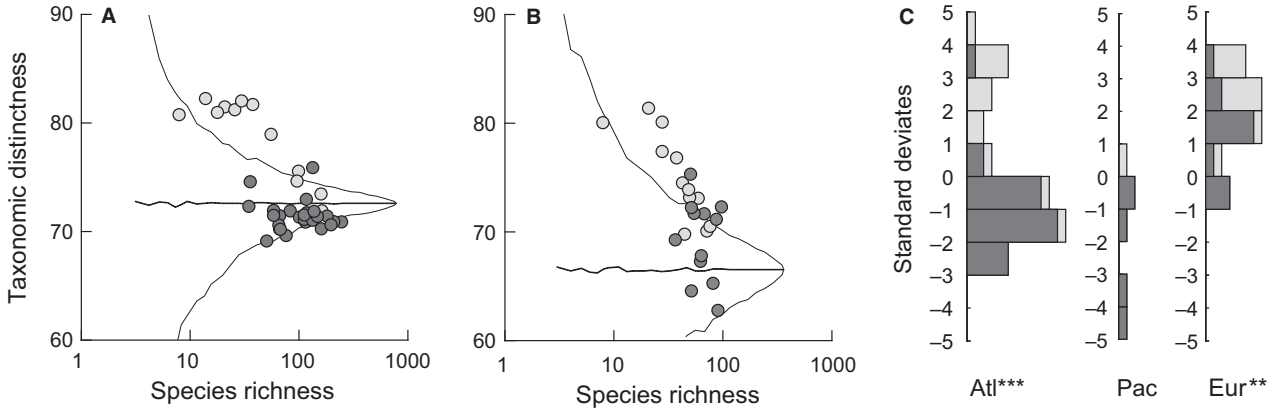

Figure 4. Average taxonomic distinctness as a function of regional species richness for glaciated (light grey) and unglaciated regions (dark grey) of (A) Atlantic and (B) European realms. The 95% confidence limits and the mean avTD, generated by randomisation, are also shown. C, Histograms showing regional standardised deviates of taxonomic distinctness, grouped for glaciated (light grey) and unglaciated regions (dark grey) of Atlantic (Atl), Pacific (Pac) and European (Eur) realms. ***$P < 0.001$, **$P < 0.01$ test for differences in deviates between unglaciated and glaciated regions.

Only 16% of the 92 late Cenozoic Atlantic realm fishes listed by Smith (1981) are extinct i.e. not found today, compared with 61% ($N = 84$) in the Pacific realm and 43% ($N = 94$) of Great Basin (Pacific realm) species (from data in Smith *et al.*, 2002). A significantly higher percentage of southern than northern Atlantic Cenozoic taxa have become extinct (23%, $N = 57$ and 0%, $N = 7$ respectively; $z = 2.49$, $P < 0.01$, one-tailed t-test). In contrast, extinction percentages in the relatively isolated drainages of the Pacific, while greater, did not differ between southern and northern taxa (59%, $N = 22$ and 58%, $N = 57$; $z = 0.10$, one-tailed t-test). Species geographic range areas increased with increasing latitude in all three realms ($r = 0.60$–0.83, all $P < 0.001$), consistent with an decreased risk of extinction in northern areas. Across realms, 49–60% of northern taxa but only 6–21% of southern taxa are migratory.

DISCUSSION

Spatial patterns

The results confirm previous assessments that the Atlantic has more freshwater fish species than the Pacific and European realms (Mahon, 1984; Moyle & Herbold, 1987; Oberdorff *et al.*, 1997; Smith *et al.*, 2010). Similar realm differences have been found in tree and herptile species (Latham & Ricklefs, 1993; Stephens & Wiens, 2003; Smith, Stephens & Wiens, 2005; Kozak & Wiens, 2012) while Haag (2010) documented low mussel species richness in the Pacific realm relative to eastern North America and noted similarities in Pacific and Eurasian richness.

Table 3. ANOVA of realm, regional connectivity, glaciation, latitude and regional area effects on regional endemicity

Variable	d.f.	MS	F-value	P-value
Realm	2	0.156	14.31	***
Regional connectivity	1	0.318	29.26	***
Glaciation	1	0.054	5.00	*
Latitude	1	0.252	26.76	***
Regional area	1	0.083	7.67	**
Error	65	0.011		
R^2		0.74		

Least squares adjusted means

	Means ± SE	N
Realm		
Atlantic	0.128 ± 0.017	42
Europe	0.239 ± 0.025	24
Pacific	0.355 ± 0.048	6
Connectivity		
Coastal	0.327 ± 0.020	41
Inland	0.154 ± 0.030	31
Glaciation		
Unglaciated	0.283 ± 0.021	47
Glaciated	0.198 ± 0.032	25

Realms with the same letter are not significantly different (Tukey HSD test).
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$. d.f., degrees of freedom; MS, mean squares; SE, standard error.

In contrast, bird and mammal richness tends to be greater in western North America (Badgley & Fox, 2000; Hawkins, Porter & Diniz-Filho, 2003). The

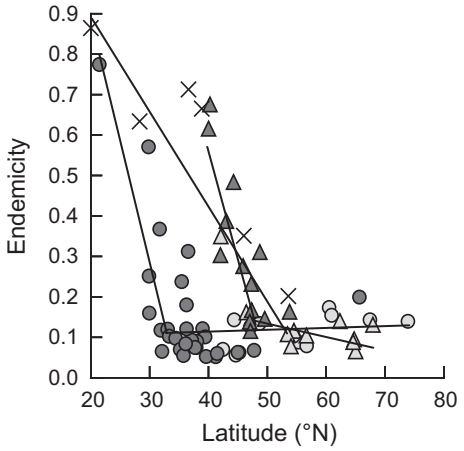

Figure 5. Regional endemicity as a function of latitude for Atlantic (circles), Pacific (crosses) and European (triangles) realms: dark fill unglaciated areas light fill glaciated areas. Lines for the Atlantic and European realms were fitted by piecewise regression.

results also show, for the first time that, across realms: (1) LRG slopes decline as connectivity declines; and (2) richness differences are greater at low latitudes.

S/G ratios, taxonomic distinctness, probability of diversification and endemicity all varied with latitude, consistent with species-rich southern regions having greater diversification rates. Most analyses show that speciation rates decline with increasing latitude (Jablonski, Roy & Valentine, 2006; April *et al.*, 2013; Rolland *et al.*, 2014). The evidence for a latitudinal gradient in net diversification rates is more equivocal (Jablonski *et al.*, 2006; Weir & Schluter, 2007; Botero *et al.*, 2014; Pyron, 2014; Rolland *et al.*, 2014), because the evidence for a latitudinal gradient in extinction rates is also contradictory (e.g. Vamosi & Vamosi, 2008; Pyron, 2014; Rolland *et al.*, 2014).

Climatic, biogeographic and evolutionary hypotheses have been proposed to account for these spatial patterns. The results strongly support the CDG framework, where climatic variability selects for dispersal and generalism, with consequences for speciation and extinction (Dynesius & Jansson, 2000; Griffiths, 2006, 2010; Jocque *et al.*, 2010).

Climatic effects

The correlation structure of climatic variables (temperature and rainfall) in the Atlantic differs from that of Pacific and Europe (Griffiths *et al.*, 2014) because of the prevailing oceanic influence in the latter realms, but climatic hypotheses make no predictions about, for example, differences in endemicity or levels of recolonization.

Converging richnesses at high latitudes suggest a climatic effect. Quaternary climate fluctuations probably caused extinctions in small-range (southern) species such as endemics (Oberdorff *et al.*, 1999; Jansson, 2003; Davies, Purvis & Gittleman, 2009; Hugueny, Movellan & Belliard, 2011). Climatic variability increases with latitude but extinction rates might be lower at high latitudes because most northern ectotherms have larger range sizes (Gaston, 2003; Griffiths, 2010; Blanchet *et al.*, 2013) and are relatively more tolerant of environmental variation than southern species (Deutsch *et al.*, 2008; Bonebrake & Mastrandrea, 2010; Clusella-Trullas, Blackburn & Chown, 2011). In connected systems, vagile northern species are more likely to move southwards during glaciations than the predominantly resident southern species. The difference in extinctions between cold- and warm-water fish taxa in the connected Atlantic regions supports this possibility: in the more isolated Pacific regions a large percentage of species became extinct regardless of latitude.

Biogeographic effects

There is extensive evidence of past vicariance and dispersal events being significant determinants of North American fish distributions (e.g. Hocutt & Wiley, 1986; Berendzen *et al.*, 2008; Schönhuth *et al.*, 2011; Bossu *et al.*, 2013) with tectonic movements, river capture, glaciation and fluctuating sea levels as important factors affecting connectivity. Consistent with the CDG framework, fish from glaciated areas exhibited higher dispersal and lower genetic diversity and divergence rates than more southern species (Bernatchez & Wilson, 1998), suggesting lower speciation rates in northern regions, a conclusion supported in a recent, more extensive, analysis (April *et al.*, 2013) and by this study.

Dispersal limitation can account for, and across-realm variation in, the LRG, with Pacific and European realms showing fewer recolonizers at low latitudes (Fig. 3). If current connectivity, rather than within catchment dispersal limitation, is the main determinant of species distributions, one might expect similarities in faunal composition to be greater and to change less rapidly with spatial separation within the Mississippi Basin than with extra-Mississippi regions. While the first expectation is, on average, met, albeit with many exceptions, the latter is not (Supporting Information, Fig. S2). Furthermore, resident Mississippi Basin species showed greater Jaccard dissimilarities and smaller range areas than migratory species, indicating a vagility effect on distribution. Some Mississippi Basin regions cluster most closely with extra-Mississippi regions (Supporting Information, Fig. S3) and there are marked differences between faunal

clusters within the catchment. These differences are a consequence of the disparate nature of the catchment in climate (mesic eastern and arid western areas) and biogeography (Supporting Information, Fig. S3), with rather different faunas found in regions occupied by the ancient Missouri, Laurentian, Teays-Mississippi and Great Plains drainages (Robison, 1986). Within the Mississippi Basin, the degree of similarity between fish faunas of the Interior Highlands corresponds to the level of connectivity between rivers (Matthews & Robison, 1998): the authors note that these upland tributaries are effectively isolated from each other by very different habitats in the lowland channels (drainage vicariance). Hence, present-day and past connectivity, habitat heterogeneity and vagility all contribute to variation in richness within the Mississippi Basin and consequently to the large number of species found there. In Europe, postglacial recolonization occurred mainly from the Ponto-Caspian area (Banarescu, 1991) but the percentage of migratory and recolonizing species was smaller in the isolated Mediterranean than other European regions.

The likelihood of recolonization varied with migratory capacity, tolerance of saline conditions and habitat preference, consistent with the findings of others (Tedesco *et al.*, 2012; Blanchet *et al.*, 2013). Hardman & Hardman (2008) noted that large-bodied ictalurid genera were species-poor and more widely distributed than the species-rich small-bodied ictalurids, a pattern consistent with the correlation between body size and dispersal (Smith, 1992; Griffiths, 2010, 2012) and hence gene flow and speciation.

Smith *et al.* (2010) argued that higher Pacific than Atlantic extinction rates resulted from uplift along the continental plate margin, thereby creating smaller, steeper catchments, and barriers to dispersal on the Pacific side. They also suggested that orogeny could account for richness differences between Mediterranean and more northern European regions but this seems less likely than in North America. The European and African tectonic plates are separated by a number of microplates in the Mediterranean Sea area which have moved in complicated ways (Windley, 1977), and the rivers draining the regions north and south of the Pyrenees, Alps, and mountains of the Balkans, unlike those in North America, do not show marked differences in size, slope or elevation.

Evolutionary effects

The rather coarse diversification measures, species/genus and probability of diversification, did not differ between Pacific and Atlantic realms. However, the Pacific showed more congeners (lower taxonomic distinctness), higher endemicity and proportionally more extinctions than the Atlantic. The drainage basins of the south-western Pacific regions have characteristically endemic faunas, with few fishes in common across basins (Minckley *et al.*, 1986). Smith *et al.* (2010) suggested that endemism in the arid southern part of the Pacific realm often results from range contraction of established species whereas Atlantic endemics are young species. Neo-endemism in freshwater fish is associated with speciation-enhancing factors (large drainage areas, climatic stability, low vagility) whereas palaeo-endemism results from isolation and extinction (Tedesco *et al.*, 2012). Smith *et al.* (2010) found slightly higher speciation rates but much higher extinction rates for freshwater fish families in Pacific than Atlantic realms. Similarly, Latham & Ricklefs (1993) concluded that tree species richness differences resulted from greater extinction rates in Pacific and European than Atlantic realms.

Diversification was lower and there are fewer species in Europe than the Atlantic. The Mediterranean Iberian, Italian and Balkan regions, with rather different fish faunas, were colonised independently from central Europe (Bianco, 1990; Banarescu, 1991). Endemics constitute a much higher percentage of species in these isolated regions compared to other European regions (medians: 45%, 3% respectively). However, regional richness declines to the west, and the western Iberian and Italian regions are relatively species-poor for their areas/latitude, suggesting dispersal limitation. The formation of the Mediterranean Sea limited colonisation from the south while northward expansion was prevented by development of mountain and marine barriers (Economidis & Banarescu, 1991).

CONCLUSION

The LRG potentially reflects the greater time-for-speciation in more amenable, usually southern, environments (Stephens & Wiens, 2003; Mittelbach *et al.*, 2007). However, while the northern Beringian glacial refuge does contain a number of distinctive forms of sub-specific status (Lindsey & McPhail, 1986), overall species richness there is no higher than in adjacent, previously glaciated, regions. In contrast, richness differences between Pacific and Atlantic realms are greater at low latitudes: the relatively flat Pacific richness gradient is due to higher extinction rates and to less recolonization from southern regions. While diversification rates are greater at low latitudes, the out-of-the-tropics model is not supported as tropical taxa have not penetrated far into North America, and the freshwater fish richness gradient there is essentially extra-tropical. More generally, the LRG is not due to southern, though

not necessarily tropical, species extending northwards but, rather, to postglacial recolonization of northern areas by southerly displaced northern species. The Wallace model (Roy & Goldberg, 2007), assumes that the richness gradient is largely a consequence of higher polar extinction rates, with speciation rates showing less latitudinal change: small-range (endemic) species probably have suffered higher extinction rates in northern latitudes but large-ranged northern taxa have not. The freshwater fish richness gradient in North America and Europe is driven by the time available for postglacial recolonization and differences in dispersal ability, with richness differences across realms reflecting differences in speciation, extinction and connectivity.

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REFERENCES

April J, Hanner RH, Mayden RL, Bernatchez L. 2013. Metabolic rate and climatic fluctuations shape continental wide pattern of genetic divergence and biodiversity in fishes. *PLoS ONE* **8:** e70296.

Badgley C, Fox DL. 2000. Ecological biogeography of North American mammals: species density and ecological structure in relation to environmental gradients. *Journal of Biogeography* **27:** 1437–1467.

Banarescu P. 1989. Zoogeography and history of the freshwater fish fauna of Europe. In: Holcik J, ed. *The freshwater fishes of Europe*. Wiesbaden: Aula-Verlag, 88–107.

Banarescu P. 1991. *Zoogeography of fresh waters: distribution and dispersal of freshwater animals in North America and Eurasia, Vol. 2*. Wiesbaden: Aula-Verlag.

Berendzen PB, Simons AM, Wood RM, Dowling TE, Secor CL. 2008. Recovering cryptic diversity and ancient drainage patterns in eastern North America: historical biogeography of the *Notropis rubellus* species group (Teleostei: Cypriniformes). *Molecular Phylogenetics and Evolution* **46:** 721–737.

Bernatchez L, Wilson CC. 1998. Comparative phylogeography of Nearctic and Palearctic fishes. *Molecular Ecology* **7:** 431–452.

Bianco PG. 1990. Potential role of the palaeohistory of the Mediterranean and Paratethys basins on the early dispersal of Euro-Mediterranean freshwater fishes. *Ichthyological Explorations in Freshwaters* **1:** 167–184.

Blanchet S, Reyjol Y, April J, Mandrak NE, Rodríguez MA, Bernatchez L, Magnan P. 2013. Phenotypic and phylogenetic correlates of geographic range size in Canadian freshwater fishes. *Global Ecology and Biogeography* **22:** 1083–1094.

Bonebrake TC, Mastrandrea MD. 2010. Tolerance adaptation and precipitation changes complicate latitudinal patterns of climate change impacts. *Proceedings of the National Academy of Sciences of the United States of America* **107:** 12581–12586.

Bossu CM, Beaulieu JM, Ceas PA, Near TJ. 2013. Explicit tests of palaeodrainage connections of southeastern North America and the historical biogeography of Orangethroat Darters (Percidae: *Etheostoma*: *Ceasia*). *Molecular Ecology* **22:** 5397–5417.

Botero CA, Dor R, McCain CM, Safran RJ. 2014. Environmental harshness is positively correlated with intraspecific divergence in mammals and birds. *Molecular Ecology* **23:** 259–268.

Brown JH, Kodric-Brown A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* **58:** 445–449.

Burnham KP, Anderson DR. 1998. *Model selection and inference: a practical information-theoretic approach*. New York: Springer-Verlag.

Carrea C, Anderson LV, Craw D, Waters JM, Burridge CP, Parmakelis A. 2014. The significance of past interdrainage connectivity for studies of diversity, distribution and movement of freshwater-limited taxa within a catchment. *Journal of Biogeography* **41:** 536–547.

Chapman BB, Skov C, Hulthén K, Brodersen J, Nilsson PA, Hansson L-A, Brönmark C. 2012. Partial migration in fishes: definitions, methodologies and taxonomic distribution. *Journal of Fish Biology* **81:** 479–499.

Clarke R, Gorley RN. 2006. *PRIMER v6: user manual/tutorial*. Plymouth: PRIMER-E.

Clarke KR, Warwick RM. 1998. A taxonomic distinctness index and its statistical properties. *Journal of Applied Ecology* **35:** 523–531.

Clusella-Trullas S, Blackburn TM, Chown SL. 2011. Climatic predictors of temperature performance curve parameters in ectotherms imply complex responses to climate change. *American Naturalist* **177:** 738–751.

Coyne JA, Orr HA. 2004. *Speciation*. Sunderland, MA: Sinauer Associates.

Crisp MD, Laffan S, Linder HP, Monro A. 2001. Endemism in the Australian flora. *Journal of Biogeography* **28:** 183–198.

Davies TJ, Purvis A, Gittleman JL. 2009. Quaternary climate change and the geographic ranges of mammals. *American Naturalist* **174:** 297–307.

Deutsch CA, Tewksbury JJ, Huey RB, Sheldon KS, Ghalambor CK, Haak DC, Martin PR. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences of the United States of America* **105:** 6668–6672.

Dias MS, Oberdorff T, Hugueny B, Leprieur F, Jézéquel C, Cornu J-F, Brosse S, Grenouillet G, Tedesco PA, Anderson M. 2014. Global imprint of historical connectivity on freshwater fish biodiversity. *Ecology Letters* **17:** 1130–1140.

Dynesius M, Jansson R. 2000. Evolutionary consequences of changes in species geographical distributions driven by Milankovitch climate oscillations. *Proceedings of the National Academy of Sciences of the United States of America* **97:** 9115–9120.

Economidis PS, Banarescu PM. 1991. The distribution and origins of freshwater fishes in the Balkan peninsula, especially in Greece. *Internationale Revue der Gesamten Hydrobiologie* **76:** 257–283.

Etheridge EC, Adams CE, Bean CW, Durie NC, Gowans ARD, Harrod C, Lyle AA, Maitland PS, Winfield IJ. 2012. Are phenotypic traits useful for differentiating among a priori *Coregonus* taxa? *Journal of Fish Biology* **80:** 387–407.

Fleiss JL. 1973. *Statistical methods for rates and proportions*. New York: John Wiley & Sons.

Gaston KJ. 2003. *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.

Gouveia SF, Hortal J, Cassemiro FAS, Rangel TF, Diniz-Filho JAF. 2012. Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography* **35:** 104–113.

Griffiths D. 2006. Pattern and process in the ecological biogeography of European freshwater fish. *Journal of Animal Ecology* **75:** 734–751.

Griffiths D. 2010. Pattern and process in the distribution of North American freshwater fish. *Biological Journal of the Linnean Society* **100:** 46–61.

Griffiths D. 2012. Body size distributions in North American freshwater fish: large-scale factors. *Global Ecology and Biogeography* **21:** 383–392.

Griffiths D, McGonigle C, Quinn R. 2014. Climate and species richness patterns in freshwater fish in North America and Europe. *Journal of Biogeography* **41:** 452–463.

Haag WR. 2010. A hierarchical classification of freshwater mussel diversity in North America. *Journal of Biogeography* **37:** 12–26.

Hardman M, Hardman LM. 2008. The relative importance of body size and paleoclimatic change as explanatory variables influencing lineage diversification rate: an evolutionary analysis of bullhead catfishes (Siluriformes: Ictaluridae). *Systematic Biology* **57:** 116–130.

Hawkins BA, Porter EE, Diniz-Filho JAF. 2003. Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology* **84:** 1608–1623.

Hillebrand H. 2004. On the generality of the latitudinal diversity gradient. *American Naturalist* **163:** 192–211.

Hocutt CH, Wiley EO, eds. 1986. *The zoogeography of North American freshwater fishes*. New York: John Wiley & Sons.

Hugueny B, Movellan A, Belliard J. 2011. Habitat fragmentation and extinction rates within freshwater fish communities: a faunal relaxation approach. *Global Ecology and Biogeography* **20:** 449–463.

Jablonski D, Roy K, Valentine JW. 2006. Out of the tropics: evolutionary dynamics of the latitudinal diversity gradient. *Science* **314:** 102–106.

Jacquemin SJ, Pyron M. 2011. Impacts of past glaciation events on contemporary fish assemblages of the Ohio River basin. *Journal of Biogeography* **38:** 982–991.

Jansson R. 2003. Global patterns in endemism explained by past climatic change. *Proceedings of the Royal Society of London B* **270:** 583–590.

Jansson R, Rodríguez-Castañeda G, Harding LE. 2013. What can multiple phylogenies say about the latitudinal diversity gradient? A new look at the tropical conservatism, out of the tropics, and diversification rate hypotheses. *Evolution* **67:** 1741–1755.

Jocque M, Field R, Brendonck L, de Meester L. 2010. Climatic control of dispersal–ecological specialization trade-offs: a metacommunity process at the heart of the latitudinal diversity gradient? *Global Ecology and Biogeography* **19:** 244–257.

Kisel Y, Barraclough TG. 2010. Speciation has a spatial scale that depends on levels of gene flow. *American Naturalist* **175:** 316–334.

Knouft JH, Page LM. 2011. Assessment of the relationships of geographic variation in species richness to climate and landscape variables within and among lineages of North American freshwater fishes. *Journal of Biogeography* **38:** 2259–2269.

Kottelat M. 1998. Systematics, species concepts and the conservation of freshwater fish diversity in Europe. *Italian Journal of Zoology* **65:** 65–75.

Kottelat M, Freyhof J. 2007. *Handbook of European freshwater fishes*. Cornol & Berlin: Kottelat & Freyhof.

Kozak KH, Wiens JJ. 2012. Phylogeny, ecology, and the origins of climate–richness relationships. *Ecology* **93:** S167–S181.

Krug AZ, Jablonski D, Valentine JW. 2008. Species–genus ratios reflect a global history of diversification and range expansion in marine bivalves. *Proceedings of the Royal Society B* **275:** 1117–1123.

Latham RE, Ricklefs RE. 1993. Continental comparisons of temperate-zone tree species diversity. In: Ricklefs RE, Schluter D, eds. *Species diversity in ecological communities*. Chicago: University of Chicago Press, 294–314.

Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, Loreau M, Gonzalez A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters* **7:** 601–613.

Leprieur F, Olden JD, Lek S, Brosse S. 2009. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *Journal of Biogeography* **36:** 1899–1912.

Lindsey CC, McPhail JD. 1986. Zoogeography of fishes of the Yukon and Mackenzie Basins. In: Hocutt CH, Wiley EO, eds. *The zoogeography of North American freshwater fishes*. New York: John Wiley & Sons, 639–674.

Lucas MC, Baras E. 2001. *Migration of freshwater fishes*. Oxford: Blackwell Science.

Mahon R. 1984. Divergent structure in fish taxocenes of north temperate streams. *Canadian Journal of Fisheries and Aquatic Sciences* **41:** 330–350.

Maitland PS. 2000. *Guide to freshwater fish of Britain and Europe*. London: Hamlyn.

Matthews WJ, Robison HW. 1998. Influence of drainage connectivity, drainage area and regional species richness on fishes of the Interior Highlands in Arkansas. *American Midland Naturalist* **139:** 1–19.

McCune B, Mefford MJ. 2006. *PC-ORD. Multivariate analysis of ecological data*. Gleneden Beach, OR: MjM Software.

McDowall RM. 1988. *Diadromy in fishes*. London: Croom Helm.

Miller RR, Minckley WL, Norris SM. 2005. *Freshwater fishes of Mexico*. Chicago: University of Chicago Press.

Minckley WL, Hendrickson DA, Bond CE. 1986. Geography of western North American freshwater fishes: description and relationships to intracontinental tectonism. In: Hocutt CH, Wiley EO, eds. *The zoogeography of North American freshwater fishes*. New York: John Wiley & Sons, 519–613.

Mittelbach GG, Schemske DW, Cornell HV, Allen AP, Brown JM, Bush MB, Harrison SP, Hurlbert AH, Knowlton N, Lessios HA, McCain CM, McCune AR, McDade LA, McPeek MA, Near TJ, Price TD, Ricklefs RE, Roy K, Sax DF, Schluter D, Sobel JM, Turelli M. 2007. Evolution and the latitudinal diversity gradient: speciation, extinction and biogeography. *Ecology Letters* **10:** 315–331.

Moyle PB, Herbold B. 1987. Life-history patterns and community structure in stream fishes of western North America: comparisons with eastern North America and Europe. In: Matthews WJ, Heins DC, eds. *Community and evolutionary ecology of North American stream fishes*. Norman, OK: University of Oklahoma Press, 25–32.

Nekola JC, White PS. 1999. The distance decay of similarity in biogeography and ecology. *Journal of Biogeography* **26:** 867–878.

Northcote TG. 1997. Potamodromy in Salmonidae - living and moving in the fast lane. *North American Journal of Fisheries Management* **17:** 1029–1045.

Oberdorff T, Hugueny B, Guégan JF. 1997. Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between western Europe and North America. *Journal of Biogeography* **24:** 461–467.

Oberdorff T, Lek S, Guégan JF. 1999. Patterns of endemism in riverine fish of the northern hemisphere. *Ecology Letters* **2:** 75–81.

Oberdorff T, Tedesco PA, Hugueny B, Leprieur F, Beauchard O, Brosse S, Dürr HH. 2011. Global and regional patterns in riverine fish species richness: a review. *International Journal of Ecology* **2011:** 967631.

Padial AA, Ceschin F, Declerck SA, De Meester L, Bonecker CC, Lansac-Toha FA, Rodrigues L, Rodrigues LC, Train S, Velho LF, Bini LM. 2014. Dispersal ability determines the role of environmental, spatial and temporal drivers of metacommunity structure. *PLoS ONE* **9:** e111227.

Page LM, Burr BM. 1991. *A field guide to freshwater fishes of North America north of Mexico*. Boston: Houghton Mifflin Company.

Pyron RA. 2014. Temperate extinction in squamate reptiles and the roots of latitudinal diversity gradients. *Global Ecology and Biogeography* **23:** 1126–1134.

R Development Core Team. 2013. *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Roberts N. 1998. *The Holocene: an environmental history*. Oxford: Blackwell.

Robison HW. 1986. Zoogeographic implications of the Mississippi River Basin. In: Hocutt CH, Wiley EO, eds. *The zoogeography of North American freshwater fishes*. New York: John Wiley & Sons, 267–285.

Rolland J, Condamine FL, Jiguet F, Morlon H. 2014. Faster speciation and reduced extinction in the tropics contribute to the mammalian latitudinal diversity gradient. *PLoS Biology* **12:** e1001775.

Ross ST. 2013. *Ecology of North American freshwater fishes*. Berkeley: University of California Press.

Ross ST, Matthews WJ. 2014. Evolution and ecology of North America fish assemblages. In: Warren ML, Burr BM, eds. *Freshwater fishes of North America*. Baltimore: Johns Hopkins University Press, 1–48.

Roy K, Goldberg EE. 2007. Origination, extinction, and dispersal: integrative models for understanding present-day diversity gradients. *American Naturalist* **170:** S71–S83.

Schleuter D, Daufresne M, Veslot J, Mason NWH, Lanoiselée C, Brosse S, Beauchard O, Argillier C. 2012. Geographic isolation and climate govern the functional diversity of native fish communities in European drainage basins. *Global Ecology and Biogeography* **21:** 1083–1095.

Schönhuth S, Blum MJ, Lozano-Vilano L, Neely DA, Varela-Romero A, Espinosa H, Perdices A, Mayden RL. 2011. Inter-basin exchange and repeated headwater capture across the Sierra Madre Occidental inferred from the phylogeography of Mexican stonerollers. *Journal of Biogeography* **38:** 1406–1421.

Smith GR. 1981. Late Cenozoic freshwater fishes of North America. *Annual Review of Ecology and Systematics* **12:** 163–193.

Smith GR. 1992. Phylogeny and biogeography of the Catostomidae, freshwater fishes of North America and Asia. In: Mayden RL, ed. *Systematics, historical ecology, and North American freshwater fishes*. Stanford: Stanford University Press, 778–826.

Smith GR, Badgley C, Eiting TP, Larson PS. 2010. Species diversity gradients in relation to geological history in North American freshwater fishes. *Evolutionary Ecology Research* **12:** 693–726.

Smith GR, Dowling TE, Gobalet KW, Lugaski T, Shiozawa DK, Evans RP. 2002. Biogeography and timing of evolutionary events among Great Basin fishes. In: Hershler R, Madsen DB, Currey DR, eds. *Great basin aquatic systems history. Smithsonian Contributions to the Earth Sciences* **33:** 175–234.

Smith ML, Miller RR. 1986. The evolution of the Rio Grande Basin as inferred from its fish fauna. In: Hocutt CH, Wiley EO, eds. *The zoogeography of North American freshwater fishes*. New York: John Wiley & Sons, 457–485.

Smith RJF. 1991. Social behaviour, homing and migration. In: Winfield IJ, Nelson JS, eds. *Cyprinid fishes: systematics, biology and exploitation*. London: Chapman & Hall, 509–529.

Smith SA, Stephens PR, Wiens JJ. 2005. Replicate patterns of species richness, historical biogeography, and phylogeny in holarctic treefrogs. *Evolution* **59:** 2433–2450.

Stephens PR, Wiens JJ. 2003. Explaining species richness from continents to communities: the time-for-speciation effect in emydid turtles. *American Naturalist* **161:** 112–128.

Sullivan SMP, Watzin MP. 2009. Stream–floodplain connectivity and fish assemblage diversity in the Champlain Valley, Vermont, U.S.A. *Journal of Fish Biology* **74:** 1394–1418.

Tedesco PA, Leprieur F, Hugueny B, Brosse S, Dürr HH, Beauchard O, Busson F, Oberdorff T. 2012. Patterns and processes of global riverine fish endemism. *Global Ecology and Biogeography* **21:** 977–987.

Tisseuil C, Cornu J-F, Beauchard O, Brosse S, Darwall W, Holland R, Hugueny B, Tedesco PA, Oberdorff T. 2013. Global diversity patterns and cross-taxa convergence in freshwater systems. *Journal of Animal Ecology* **82:** 365–376.

Vamosi JC, Vamosi SM. 2008. Extinction risk escalates in the tropics. *PLoS ONE* **3:** e3886.

Weir JT, Schluter D. 2007. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315:** 1574–1576.

Wiens JJ, Ackerly DD, Allen AP, Anacker BL, Buckley LB, Cornell HV, Damschen EI, Davies TJ, Grytnes J-A, Harrison SP, Hawkins BA, Holt RD, McCain CM, Stephens PR. 2010. Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters* **13:** 1310–1324.

Wiens JJ, Sukumaran J, Pyron RA, Brown RM. 2009. Evolutionary and biogeographic origins of high tropical diversity in Old World frogs (Ranidae). *Evolution* **63:** 1217–1231.

Windley BF. 1977. *The evolving continents*. Chichester: John Wiley & Sons.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Figure S1. The percentages of species of South American origin declines to the north for Atlantic (circles) and Pacific (crosses) drainages.

Figure S2. Jaccard distances as a function of spatial separation for pairs of regions, when both regions are within the Mississippi Basin (circles) and when one region is inside and one outside the Mississippi Basin (crosses). Fifteen per cent of cross-Basin region distances are smaller than the predicted within-Basin values while 26% of within-Basin values are greater than the predicted cross-Basin values.

Figure S3. Jaccard distances between the regional fish faunas of North America, clustered by the flexible β (−0.25) method. Note that Jaccard distances between the Ohio/Tennessee and central Mississippi regional clusters of the Mississippi Basin were as great as those between the regions comprising the arctic (Mackenzie, Yukon) and subtropical clusters (Mexico, Rio Grande) of the Atlantic realm, and the Missouri regions differed even more from the rest of the Mississippi Basin (Jaccard distances 1.30, 1.35 and 1.59 respectively). The lines and letters to the left of the figure indicate some of the Mississippi Basin regions associated with particular Pliocene drainages (H = Hudson Bay/Arctic, P = Great Plains, T = Teays-Mississippi), from Figure 9.3 in Hocutt & Wiley (1986).

Table S1. Numbers of species in the categories listed in Table 1.

Table S2. ANOVA of realm, glaciation, regional species richness on standardised deviates from null model expectation of taxonomic distinctness.

Table S3. Analysis of deviance of continent, and latitude effects on probability of diversification.